ATOLL RESEARCH BULLETIN

NO. 476

DIVERSITY OF SPONGE FAUNA IN MANGROVE PONDS, PELICAN CAYS, BELIZE

BY

KLAUS RÜTZLER, MARIA CHRISTINA DIAZ, ROB W.M. VAN SOEST, SVEN ZEA, KATHLEEN P. SMITH, BELINDA ALVAREZ, AND JANIE WULFF

ISSUED BY
NATIONAL MUSEUM OF NATURAL HISTORY
SMITHSONIAN INSTITUTION
WASHINGTON, D.C., U.S.A.
MARCH 2000

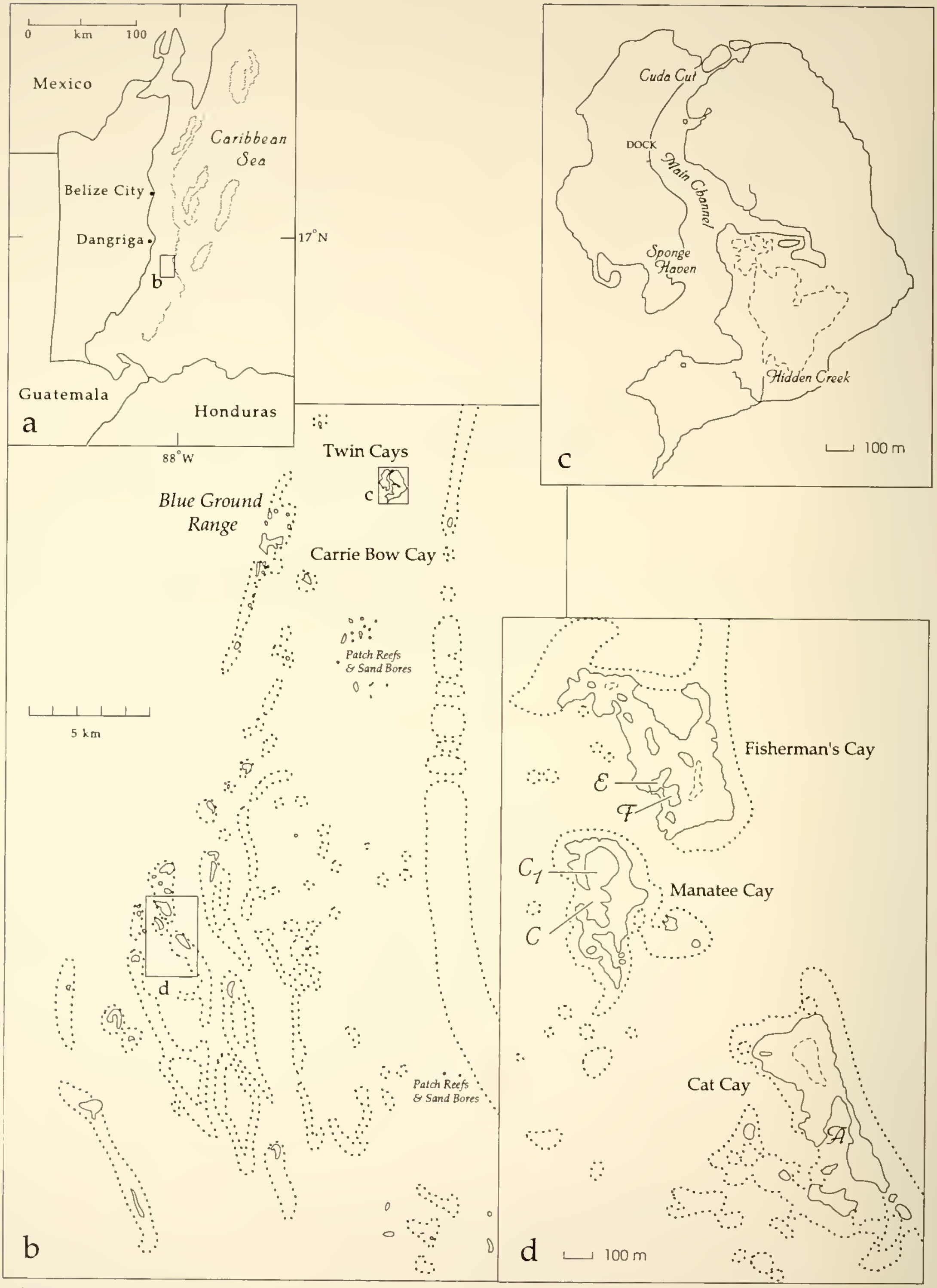

Figure 1. Map of Belize (a) with enlarged research areas: southern barrier reef lagoon (b), Twin Cays (c), and portion of Pelican Cays (d).

DIVERSITY OF SPONGE FAUNA IN MANGROVE PONDS, PELICAN CAYS, BELIZE

BY

KLAUS RÜTZLER,[1] MARIA CRISTINA DIAZ,[2] ROB W. M. VAN SOEST,[3] SVEN ZEA,[4] KATHLEEN P. SMITH,[1] BELINDA ALVAREZ,[5] and JANIE WULFF[6]

ABSTRACT

Mangrove-fringed ponds in the Pelican Cays, Belize, support an uncommonly diverse population of colorful and large sponges. Sponge species and abundance were determined for ponds at Cat Cay (Pond A), Manatee Cay (C), and Fisherman's Cay (E and F) and compared with the sponge fauna of more typical and common mangrove habitats elsewhere in the Belize lagoon, one at Blue Ground Range and three at Twin Cays, 10–15 km to the north. The seven habitats differ in species composition and hierarchy, the Pelican Cays ponds being by far the most species-rich, with an unusually high number of poorly known or undescribed taxa.

The principal factors promoting diversity in the Pelicans are abundance of solid substrates (mangrove stilt roots, extended peat banks), low turbidity, and proximity of sponge-rich coral reefs. The topography of deep ponds alternating with steep coral ridges helps contain fine sediments and prevents resuspension and silting during storms without blocking water exchange, which is necessary for importing nutrients and flushing waste. Blue Ground Range is the most sediment-exposed habitat and supports selected silting-resistant species. Twin Cays are intermediate in sedimentation and species numbers and suffer the most physical disturbance from boating and fishing.

---

[1]Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560-0163, USA.

[2]Ocean Sciences Department, University of California at Santa Cruz, Santa Cruz, CA 95054, USA.

[3]Institute for Systematics and Ecology, University of Amsterdam, P.O. Box 94766, 1090 GT Amsterdam, The Netherlands.

[4]Universidad Nacional de Colombia (Departamento de Biologia), INVEMAR, Apartado 10-16, Santa Marta, Colombia.

[5]National Institute of Water and Atmospheric Research, Ltd., P.O. Box 14-901, Kilbirnie, New Zealand.

[6]Department of Biology, Middlebury College, Middlebury, VT 05753, USA.

INTRODUCTION

Biologists and geologists associated with the Smithsonian National Museum of Natural History have been studying the tropical marine shallow-water communities of Belize, Central America, for more than 25 years. Most of their research has been sponsored by the Caribbean Coral Reef Ecosystems (CCRE) program and has concentrated on the barrier reef near Carrie Bow Cay (16°48'N, 88°05'W), the location of the program's field station (Rützler and Macintyre, 1982), and on the mangrove ecosystem of Twin Cays (Rützler and Feller, 1996). During the early 1990s, some program participants shifted their attention to the rich benthic communities associated with coral ridges and mangrove roots of mangrove-fringed ponds of the Pelican Cays, an archipelago of mangrove islands in the southern Belize shelf lagoon, just 16 km southwest of Carrie Bow Cay. Sponges, algae, and ascidians, are among the most abundant sessile organisms there, densely overgrowing most exposed solid substrates, and are notable for their stunning colors and bizarre shapes. All who have studied sponges in shallow waters throughout the Caribbean have been impressed by the diversity of sponges found in the Pelican Cays.

To document this phenomenon, we surveyed species richness and abundance in these islands and compared them with the sponge fauna of similar environments at Twin Cays and Blue Ground Range, two groups of mangrove cays 3 km northwest and 6.5 km west, respectively, of the Carrie Bow field station and well known from previous studies. Because taxonomic work on the sponges is still in progress, we restrict our observations to the common and systematically recognized forms. A revision of the species collected will be published as part of a separate monograph.

METHODS AND STUDY AREA

Sponges were collected in separate bags by snorkeling and free-diving and returned to the Carrie Bow field station in buckets of fresh seawater. Where possible, specimens were photographed undisturbed in their natural setting before collecting using a Nikonos camera with close-up lens and one or two small strobe units (Ikelite) angled 45° to the camera axis. Specimens were also photographed in the laboratory submersed in a tray with seawater, with a Nikon F with Micronikkor macro lens on a copy stand and two Vivitar strobes at 45°. After a preliminary morphological study, small samples were removed for skeleton mounts and specimens were fixed in 10% formalin in seawater (12–24 h) and transferred to 80% ethylene alcohol for transport and storage.

At the field station, a compound microscope was used to examine skeleton structure in dried hand sections cleared in Permount medium (Fischer Scientific). Spicule types were determined after dissolving samples in concentrated laundry bleach (5% sodium hypochlorite). Abundance estimates were based on the consensus of six collectors (Alvarez, Diaz, Van Soest, Smith, Wulff, and Zea) after each collecting trip in August 1997. The method used (1 = very common; 2 = common–rare; 3 = very rare), though subjective, captured the quantity and size of individuals a casual observer might readily notice. A small but "common" sponge (one appearing in many places) may have a similar score as a larger but less common species, whereas a single, very large specimen would still be considered a "rare" species. In comparing species composition, we applied Sorensen's formula (Pielou, 1992) because it compensates for very different species numbers in various locations by doubling the number of shared taxa: 2a/2a + b + c (where a = number of species common to both locations; b, c = number of species occurring only in one of the compared samples). Estimates of pond size were made using a planimeter on maps drawn from aerial photographs and improved and scaled by ground-truthing. Some depth measurements were made using a hand-held Scubapro PDS-2 dive sonar and converting data from feet to meters.

The general setting of the Pelican Cays (16°39.8'N, 88°11.5'W) and topography and major biological components of the ponds are described by Macintyre et al. (this volume). For consistency, we use their term "pond" (designated by a letter) rather than "lagoon" to indicate the reduced water exchange with the outside by entrance-blocking coral ridges, and to avoid confusion with the principal barrier-reef lagoon. As mentioned earlier, the Twin Cays and Blue Ground Range near Carrie Bow Cay were also surveyed in this study. The mangroves, historical development, and biology of Twin Cays (16°50.0'N, 88°06.3'W) have been described by Rützler and Feller (1987, 1996), and some work has already been done on the sponge biota, including the families Chalinidae (de Weerdt et al., 1991) and Mycalidae (Hajdu and Rützler, 1998). The latter study includes samples from Blue Ground Range (16°48.6'N, 88°08.9'W), an extensive mangrove development at the inner (landward) edge of the barrier-reef shelf.

RESULTS

Four ponds enclosed or partly enclosed by red mangroves (*Rhizophora mangle*) were investigated at three Pelican Cays islands: Cat, Manatee, and Fisherman's Cays (Fig. 1, Table 1). These sites were chosen because of their reportedly rich sponge fauna (I. Goodbody, personal communication) and because of time constraints. Other ponds in the Pelican group also contain sponges (Goodbody, this volume; Macintyre et al., this volume) but they are not nearly as diverse and are more similar in character to the majority of mangrove cays elsewhere in the Belize shelf lagoon. Comparative collections were made at four other sites: one at Blue Ground Range, the other three at Twin Cays.

Description of Sites

Cat Cay. Pond A, located at Cat Cay, is a deeply cut oval bay stretching north-south and has a shallow coral ridge and two small mangrove islets blocking most of the main entrance, which faces west and south. The coral ridge rises steeply from the sea floor and levels off at an average depth of about 0.5 m (mean tide level). The pond is about 285 x 90 m and covers more than 29,000 m^2 (2.9 ha). The circumference of the pond, including the coral ridge, measures more than 600 m. About 41% of the perimeter consists primarily of coral, coral rubble, and coral-covered mangrove roots; 43% is a red-mangrove shoreline with exposed and submerged roots and stilt roots; the remaining 16% is muddy intertidal or other substrate covered by algae. The coral ridge at the entrance and the coral rubble, mangrove roots, and peat banks lining the shallow margin provide a solid substrate relatively free of sediment for sponges and ascidians, the principal sessile filter feeders in Pond A. Despite the lush mangrove growth and the abundance of fine sediments, the water along the red-mangrove shoreline is extremely clear. The maximum recorded depth (at the bottom of the inner slope of the coral ridge) is 14 m; the muddy bottom near the center of the pond reaches 10.5 m.

Table 1. List, distribution, and estimated abundance of sponges in localities surveyed (1=rare, 2=common, 3=abundant).

Taxa	Pelican Cays			Blue Ground Range	Twin Cays		
	Cat	Manatee	Fisherman's		Hidden Creek	Cuda Cut	Sponge Haven
Homosclerophorida							
Plakinidae							
Plakina jamaicensis Lehnert & van Soest	1						
Plakinastrella onkodes Uliczka	1						
Plakortis halichondrioides? (Wilson)	2	1	2			2	1
Oscarella sp. 1		1					
Oscarella sp. 2		1	1				
Oscarella sp. 3		1					
Spirophorida							
Tetillidae							
Cinachyrella apion (Uliczka)		1	3	1	2	1	1
Astrophorida							
Ancoriniidae							
Ecionemia dominicana (Pulitzer-Finali)	1	1					
Myriastra kallitetilla de Laubenfels							1
Geodiiae							
Geodia gibberosa (Lamarck)		1	1				
Geodia papyracea Hechtel	1				3	2	3
Geodia sp.	1						
Pachastrellidae							
Dercitus sp.			1				
Hadromerida							
Chondrillidae							
Chondrilla nucula Schmidt[a]	2	3	3	1	1	2	2
Chondrosia collectrix (Schmidt)	1	1	1				
Clionidae							
Anthosigmella varians (Duch. & Mich.)		3	1				1
Cliona caribbaea Carter	1						
Cliona sp.			1				
Placospongiidae							
Placospongia intermedia Sollas	2	3	2				
Spirastrellidae							
Diplastrella megastellata Hechtel	1						
Spirastrella coccinea (Duch. & Mich.)	1						
S. mollis Verrill	2	3	2				2
Suberitidae							
Aaptos duchassaingi (Topsent)		1					
Terpios aurantiaca Duch. & Mich.		1					
T. fugax Duch. & Mich.	1						
T. manglaris Rützler & Smith	2	3		1			1
Terpios sp. 1	2	1					
Terpios sp. 2		1	2				

Table 1.--continued

Taxa	Pelican Cays			Blue Ground Range	Twin Cays		
	Cat	Manatee	Fisherman's		Hidden Creek	Cuda Cut	Sponge Haven
Suberitidae sp.			1				
Tethyiidae							
Tethya actinia de Laubenfels	1	3	1		1		1
T. aff. *actinia* sp. 1	1	1		1			
T. aff. *actinia* sp. 2	1	3					
T. aff. *actinia* sp. 3		1					
Timeiidae							
Paratimea? sp.						1	
Timea unistellata Topsent	1						
Agelasida							
Agelasiidae							
Agelas conifera (Schmidt)	1						
Poecilosclerida							
Anchinoidae							
Phorbas amaranthus Duch. & Mich.	2	1	1	1			
Coelosphaeridae							
Coelosphaera raphidifera Hechtel	1						
Lissodendoryx colombiensis Zea & van Soest	2	1	1	3			
L. aff. *isodictyalis* (Carter)		2	2	1	3	3	
L. sigmata (de Laubenfels)							1
Crambeidae							
Monanchora arbuscula (Duch. & Mich.)	3	3	1				
Monanchora sp.	2	1	1				
Desmapsamma anchorata (Carter)[a]	3	1	2				
Desmacellidae							
Biemna caribea Pulitzer-Finali					3	1	1
Desmacella janiae Verrill				1			
D. meliorata Wiedenmayer			1				
Desmacella sp.				1			
Neofibularia nolitangere (Duch. & Mich.)	1		1				
Hymedesmiidae							
Hymedesmia sp.		1					
Iophonidae							
Acarnus sp.				3			
Microcionidae							
Artemisina melana van Soest	3	2	2	2			
Clathria affinis (Topsent)	2	2					
C. echinata (Alcolado)	2						
C. schoenus (de Laubenfels)	3	3	3	3			1
C. aff. *schoenus* (de Laubenfels)							1
C. spinosa (Wilson)	1						
C. venosa (Alcolado)	1	3	3	2	1	2	3
C. virgultosa (Lamarck)							1
Clathria sp. 1					1		
Clathria sp. 2	1						

Table 1.--continued

	Pelican Cays				Twin Cays		
Taxa	Cat	Manatee	Fisherman's	Blue Ground Range	Hidden Creek	Cuda Cut	Sponge Haven
Mycalidae							
Mycale angulosa (Duch. & Mich.)		2		1			
M. arenaria Hajdu & Desqueyroux-Faundez	1	2	2	2			
M. arndti van Soest		1					
M. citrina Hajdu & Rützler		1	2			2	
M. escarlatei Hajdu et al.			1				
M. laevis (Carter)[a]	3	3	3	3			1
M. carmigropila Hajdu & Rützler						1	1
M. laxissima (Duch. & Mich.)	2	1				2	
M. magniraphidifera van Soest							1
M. aff. *magniraphidifera* van Soest					2	1	1
M. microsigmatosa Arndt	2	3	3	3		2	3
M. aff. *microsigmatosa* Arndt	1						
Mycale sp. 1	2		1				
Mycale sp. 2							1
Mycale sp. 3						1	
Mycale sp. 4		1					
Mycale sp. 5		1					
Paresperella sp.	1	1		1			
Myxillidae							
Iotrochota birotulata (Higgin)	3	3	3	1			
Iotrochota sp.				2			
Phoriospongidae							
Strongylacidon sp.	2		1				
Raspailiidae							
Ectyoplasia ferox (Duch. & Mich.)	2		1				
Eurypon laughlini Diaz et al.				3			
Eurypon sp.	1						
Tedanidae							
Tedania ignis (Duch. & Mich.)	1	2	2	3	3	3	3
T. aff. *ignis* (Duch. & Mich.)	2	2	1				
Halichondrida							
Axinellidae							
Pseudaxinella? spp. aff. *zeai* Alvarez et al.	2		1				
Ptilocaulis walpersi (Duch. & Mich.)			1				
Dictyonellidae							
Dictyonella sp.							1
Scopalina hispida (Hechtel)	1		3				
S. ruetzleri (Wiedenmayer)[a]	3	3	3	2	1	1	2
Scopalina? sp.		1					
Ulosa funicularis Rützler[a]	2						
Halichondriidae							
Amorphinopsis sp.1	1		2		3		
Amorphinopsis sp. 2		1	1				

Table 1.--continued

Taxa	Pelican Cays: Cat	Pelican Cays: Manatee	Pelican Cays: Fisherman's	Blue Ground Range	Twin Cays: Hidden Creek	Twin Cays: Cuda Cut	Twin Cays: Sponge Haven
Ciocalypta? sp.			1				
Halichondria magniconulosa? Hechtel			2		3	2	3
H. poa? De Laubenfels				3			3
Hymeniacidon caerulea Pulitzer-Finali	1	1					
Myrmekioderma rea (de Laubenfels)	1	1					
Topsentia ophiraphidites de Laubenfels	1	1	2				
Haplosclerida							
Callyspongiidae							
Callyspongia fallax Duch. & Mich.[a]	2		2				
C. vaginalis (Lamarck)		1					
Callyspongia sp.		1					
Chalinidae							
Halicona caerulea (Hechtel)				1			
H. curacaoensis (van Soest)	1	1	3		2		2
H. aff. *curacaoensis* (van Soest)	1	3	2	1			
H. implexiformis (Hechtel)		1	2	1	3	2	1
H. aff. *implexiformis* (Hechtel)		1					
H. magnifica de Weerdt et al.		1		1	1		
H. manglaris Alcolado	2	1	2	1	2	2	3
H. mucifibrosa de Weerdt et al.				2		3	3
H. pseudomolitba de Weerdt et al.					2		1
H. tubifera (George & Wilson)		1	1	1	2		2
H. aff. *tubifera* (George & Wilson)				2			
H. twincayensis de Weerdt et al.				1	1		
Haliclona sp. 1		1		1			
Haliclona sp. 2				1			
Haliclona sp. 3						1	1
Haliclona sp. 4		1					
Haliclona sp. 5		1					
Haliclona sp. 6							1
Haliclona sp. 7		3					
Haliclona sp. 8		1					
Haliclona sp. 9			1				
Haliclona sp. 10			1	1			
Haliclona sp. 11		1					
Haliclona sp. 12				1			
Chalinidae sp.		1	1				
Niphatidae							
Amphimedon compressa Duch. & Mich.	3	1		1			
A. erina (de Laubenfels)	3	3	2			1	1
A. aff. *erina* (de Laubenfels)	2	3					
Gellius sp.		1					
Niphates digitalis (Lamarck)	2						
N. erecta Duch. & Mich.	2	1					
Niphates sp.	1						

Table 1.--continued

	Pelican Cays				Twin Cays		
Taxa	Cat	Manatee	Fisherman's	Blue Ground Range	Hidden Creek	Cuda Cut	Sponge Haven
Petrosiidae							
Petrosia weinbergi (van Soest)	1						
Strongylophora davilai Alcolado	1	1					
Xestospongia carbonaria (Lamarck)	3	3	3				
X.? caycedoi Zea & van Soest	1	1					
X. muta (Schmidt)[a]	1	1	1				
X. proxima (Duch. & Mich.)	1	3	1				
X. subtriangularis (Duchassaing)			1				
Phloeodictyidae							
Aka siphona (de Laubenfels)	1						
Aka sp.		1					
Calyx podatypa (de Laubenfels)	2	2		2			3
Oceanapia sp. 1	1						
Oceanapia sp. 2		1					
Dictyoceratida							
Irciniidae							
Fasciospongia? sp.		1					
Hyrtios proteus Duch. & Mich.	2	2	1	3	1	1	3
Hyrtios sp.			1			1	
Ircinia campana (Lamarck)				3			
I. felix (Duch. & Mich.)	2	2	1	3			1
I. strobilina (Lamarck)	1	2	1	1			1
Ircinia sp. 1		1		1			
Ircinia sp. 2		2					
Ircinia sp. 3				1			
Ircinia sp. 4				1			
Smenospongia aurea (Hyatt)	1						
Spongiidae							
Cacospongia sp.				1			
Spongia obscura Hyatt	1	2	3	1		1	
S. tubulifera Lamarck[a]	3	3	3	1	2	1	3
Dendroceratida							
Dysideidae							
Dysidea. etheria de Laubenfels	2		3			1	
D. janiae (Duch. & Mich.)				3			
Dysidea sp. 1			3		2		
Dysidea sp. 2			1				
Darwinellidae							
Aplysilla sp. 1	2	2					
Aplysilla sp. 2	1						
Aplysilla sp. 3			1				
Chelonaplysilla aff. *erecta* (Row)	2	2	3	1			
Darwinella rosacea Hechtel			1			1	
Pleraplysilla sp.				1			

Table 1.--continued

	Pelican Cays				Twin Cays		
Taxa	Cat	Manatee	Fisherman's	Blue Ground Range	Hidden Creek	Cuda Cut	Sponge Haven
Halisarcidae							
Halisarca caerulea Vacelet	2	2	2	1			
Halisarca sp.			3		2		
Verongida							
Aplysinidae							
Aiolochroia crassa (Hyatt)	2		1				
Aplysina archeri Higgin		1					
A. fistularis (Pallas)	1	1					
A. fulva (Pallas)	3	1	3				
Verongula rigida Esper	2	2	1				
Calcarea							
Clathrina aff. *coriacea* (Montagu)			2		2	3	2
Sycon sp.				1	1		1
Total number of species per locality	90	95	77	54	26	29	42
Species per region		147		54		57	

[a]See Plate 2

Before entering the lagoon by swimming across the coral ridge, one encounters an unexpectedly steep outer slope that rises from a sandy bottom at 22 m and is covered by lettuce coral (*Agaricia tenuifolia*) with isolated stands of staghorn coral (*Acropora cervicornis*). In 1994, many of the *A. cervicornis* were partly bleached, possibly by white-band disease. Some isolated *Agaricia* blades were also freshly bleached, perhaps as a result of starfish (*Oreaster*) feeding, which was occasionally observed in 1997. Several large sponges are attached to the dead coral and coral rubble in this area. Clusters of large barrel sponges, dark purplish brown *Xestospongia muta* (Plate 2b), form several reef-like islands on the lower slope between 6 and 15 m, where coral growth is less lush and interspersed with sand, coral rubble, and patches of turtle grass (*Thalassia testudinum*). Associated with *Xestospongia* are long, intertwined ropy sponges, blackish green *Iotrochota birotulata,* crimson *Amphimedon compressa,* and ochre-yellow *Aplysina fulva.* Other large sponges present on the slope are tall tubes of gray *Niphates digitalis* and blackish red *Mycale laxissima,* brown bowl-shaped *Ircinia campana,* and massive blackish gray *I. strobilina.*

In the shallow parts, and on top of the *Agaricia* ridge, coral is partly overgrown by extensive patches of greenish brown *Chondrilla nucula* (Plate 2a), a leathery and tough encrusting sponge with a very smooth, slick surface, which is known to be an aggressive competitor for space (Vicente, 1990). (This sponge may well be an undescribed species of *Chondrilla* because its growth habit and ecology are very different from that of the familiar *C. nucula*, a Mediterranean relative, although the siliceous spicules, spherasters, are indistinguishable between the two.) Another green encrusting sponge in this habitat, *Ulosa* *funicularis* (Plate 2a), is darker (with a grayish tinge) and soft, and has thin whip-like processes (Rützler, 1981). Both harbor large numbers of unicellular cyanobacteria and thus are photosynthetic species (Rützler, 1990). These two crustose species—along with ropy, yellow *Aplysina fulva* and blackish *Iotrochota birotulata,* tube clusters of violet to pink *Callyspongia fallax,* and layers of a colonial gray-green zoanthid, *Zoanthus* sp.—also grow on loose coral plates and seem to help stabilize them. Rützler (1965) introduced the term "Kittschwämme" ("putty" sponges) to describe this sponge-mediated binding of reef coral and rubble, a phenomenon also described by Wulff and Buss (1979) and Wulff (1984). Other sponges attached to *Agaricia* coral plates on the ridge are encrusting red *Monanchora arbuscula* and cushion-shaped yellow *Mycale laevis* (Plate 2c,d), as on open reefs, attached to the underside of plates, and blackish-olive *Xestospongia carbonaria.* At least one excavating sponge, the dark brown symbiotic (with zooxanthellae) *Cliona caribbaea* is commonly found in the coral skeleton.

Moving clockwise from the ridge toward the pond, one finds red-mangrove root and rubble substrates overgrown by coral (forming *Agaricia* "mini-reefs") and by large or extensively encrusting sponges, particularly branching pink *Desmapsamma anchorata* (Plate 2c), blackish green (exuding purple stain when touched) *Iotrochota birotulata,* many covered by a yellow-orange symbiotic zoanthid (*Parazoanthus swifti*), deep orange-brown *Artemisina melana*, deep red *Mycale laxissima,* blackish *Xestospongia carbonaria,* and bright crimson *Amphimedon compressa*. Massive or thickly encrusting forms include the ubiquitous orange-red *Scopalina ruetzleri,* blackish-with-gray large (80 cm across) *Ircinia strobilina,* dark wine-red *Mycale laxissima,* sky-blue *Dysidea etheria,* and yoke-yellow *Mycale laevis* (Plate 2c,d). The most common thinly encrusting species are blue-green *Terpios manglaris,* grayish to pinkish *Clathria echinata*, and red *Monanchora arbuscula.* Massive sponges such as brown *Ircinia felix* and black *Hyrtios proteus* are often encountered on coral rubble between the mangrove fringe and stands of turtle grass. Excavating *Cliona caribbaea* occur in the same habitat.

Continuing clockwise around the pond, one finds at least 90 species, but no distinctive distributional patterns can be discerned. The species just mentioned occur here as well. The larger massive forms include the amorphous black *Spongia tubulifera*, which supports a great variety of smaller epizoic sponges, bluish-green *Amphimedon erina*, sprawling-tubular brown *Calyx podatypa*, yellow *Aiolochroia crassa* and *Verongula rigida,* branching reddish black *Artemisina melana,* and yellow-over-salmon *Clathria schoenus.* Conspicuous crusts on mangrove roots are pale-red *Spirastrella mollis,* deep red *Phorbas amaranthus*, red-granular *Mycale microsigmatosa,* and leathery blue *Halisarca caerulea.*

Manatee Cay. The sponge survey at Manatee Cay focused exclusively on the large lagoon-like "Pond C," which is actually a composite of three bays that may have evolved from separate ponds. The pond measures 333 m (N-S) x 144 m (W-E) and covers an area of 3.24 ha. Most of the 638-m long circumference is covered by a mangrove fringe. The 60-m wide entrance, which faces west, is blocked by the shallows of a coral ridge. The largest, northern lobe of the pond (which we have named C_1 and covers 1.87 ha, with 485 m of shoreline) is the richest in terms of habitat variety and populations of filter-feeding sponges and ascidians. The entrance into C_1 faces south and is narrower than the main entrance (44 m). This pond is deeper and visibility is lower than in Cat Cay's pond A. During our survey (August 5, 1997) we measured the following maximum depths (by hand-held sonar) and average horizontal visibility at the surface (Secchi disk):

Just west outside main entrance into Pond C	15.0 m depth/8.0 m visibility
Center of northern lobe (C_1)	11.0 m depth/4.5 m visibility
Center of Pond C (east of main entrance)	10.0 m depth/6.0 m visibility
Just east of center of southern lobe	13.5 m depth/4.5 m visibility

Turning north and swimming clockwise after entering Pond C, one first encounters a muddy bottom with turtle grass and *Halimeda* algae. Sponges are associated with pieces of rubble and include brown clumps of *Anthosigmella varians*, greenish brown crusts of *Chondrilla nucula* (Plate 2a), clusters of dull green *Amphimedon erina* and brownish *Ircinia felix,* and red-orange, cake-shaped *Lissodendoryx colombiensis.* Red mangrove roots in this area support primarily the red encrusting *Mycale microsigmatosa,* branching red-blackish *Artemisina melana,* and blackish *Iotrochota birotulata.* From here on, most of the western submerged shoreline consists of more or less undercut peat banks with exposed mangrove roots and overhanging or overarching *Rhizophora* stilt roots. Both are densely carpeted by sponges and ascidians; sponges are dominant and exhibit considerable diversity in the darker parts of the undercuts where there is no competition for space from algae.

Common exposed massive species, apart from *Artemisina* and *Iotrochota,* are yellow *Aplysina fulva,* black *Spongia tubulifera* (Plate 2d) and *Hyrtios proteus,* yellow *Mycale laevis* (Plate 2c,d), some surviving half-buried in mud after having fallen off the original substrate, orange *Scopalina ruetzleri* (Plate 2e), red *Clathria schoenus,* red fire sponge *Tedania ignis,* and dark-brown *Xestospongia proxima.* Large, continuous but very thin crusts include pale red *Spirastrella mollis,* blue-green *Terpios manglaris,* and red *Monanchora arbuscula.* Smaller but diverse and abundant encrusting and cushion-shaped species occur as epizoans on other species (e.g., on Spongia tubulifera) and particularly on the back walls and ceilings of the cave-like undercuts: brown *Placospongia intermedia,* grayish *Clathria venosa,* greenish and reddish species of *Clathria* and *Mycale,* orange *Scopalina ruetzleri* (Plate 2e). Again, crusts are common in the dark zone of the caves: gray to whitish *Haliclona curacaoensis,* bluish-green *Amphimedon erina,* blackish olive *Xestospongia carbonaria,* blue *Halisarca caerulea,* and near-spherical, green and orange *Tethya actinia.* Many of the large and common species extend their distribution to the northeastern, southeastern, and southern flanks of the pond where habitats are restricted to stilt roots isolated by mud bottoms, but diversity is markedly lower then in the zone of the peat undercuts. Only a few sponge species, such as the common *Scopalina, Ircinia,* and *Tedania,* occur along the central eastern shoreline across from the main entrance.

Fisherman's Cay. Two interconnected ponds, E and F, are present here, but only E, the northern one, has an entrance to the open water. The two ponds are almost the same size and together form a figure 8: E with an area of 0.40 ha (225-m circumference), F covering 0.41 ha (227-m circumference). The longest perpendicular axis of E measures 122 x 44 m and that of F is 91 x 70 m. The only entrance from the outside is 8 m wide and up to 4 m deep; the center of pond E drops to 11 m. The *Agaricia* coral ridge has a steep slope with some conspicuous clusters of tubes of the blackish red sponge *Mycale laxissima.* There is a forest of stilt roots at the entrance and ample coarse sand made up of *Halimeda* chips. Some turtle grass, *Thalassia,* is also present, and although the slope into the pond is muddy, the water is surprisingly clear. Roots and peat banks with small undercuts at the entrance are thickly covered by algae, ascidians, and large encrusting or ropy branching sponges, particularly the orange *Scopalina ruetzleri* (Plate 2e), grayish *Clathria* *venosa,* yellow *Aplysina fulva,* and blackish *Artemisina melana.* Hanging mangrove roots backed by a vertical peat bank 1–2 m in relief, line most of the pond and provide substrate for the sessile organisms, including algae, ascidians, sponges, corals, and some octocorals. Prominent sponges are massive yellow *Mycale laevis* (Plate 2c,d), blackish *Spongia tubulifera* and *S. obscura,* ropy red *Clathria schoenus,* and encrusting brown *Chondrilla nucula* (Plate 2a) and red *Mycale microsigmatosa*. The passage connecting E and F is only 5 m wide and less than 1 m deep. Again, the roots are covered thickly by *S. ruetzleri* (Plate 2e) and draped by *A. fulva*, and coral rubble at the bottom contains a yellow excavating sponge, *Cliona* sp. Other conspicuous sponges found here are thinly encrusting grayish-yellowish *Clathria venosa,* several *Mycale* spp. (including red *M. microsigmatosa*), blue *Halisarca caerulea,* and a second tan species of *Halisarca.* Many cushion-shaped or thickly encrusting smaller species are also present, including deep purple *Chelonaplysilla* cf. *erecta,* blue and gray *Dysidea etheria* and *Dysidea* sp., blue *Haliclona curacaoensis,* blackish green *Iotrochota birotulata* and *Xestospongia carbonaria*, gray-green *Lissodendoryx* cf. *isodictyalis,* and tan, ball-shaped *Cinachyrella apion.*

Other Sites. Using the same techniques, we sampled four sites in two other mangroves, Blue Ground Range and Twin Cays. Both ranges were familiar to some of us from previous studies. They have an abundance of habitats supporting a diverse sponge fauna, and seem more typical of the thousands of mangrove cay habitats scattered throughout the Belize lagoon than in the Pelicans. The primary difference is that most of the mangrove islands do not have the deep, clear, isolated ponds characteristic of the Pelican Cays but instead have a system of tidal channels and shallow lakes with high turbidity from fine sediments that are suspended and redeposited with each tidal cycle and storm event. The sponges sampled are listed in Table 1.

Blue Ground Range (locally also known as Cockney Range) is a series of mangrove islands lying in a line oriented north to south. Our site ("Center of Origin"; Hajdu and Rützler, 1998) is an extensive, deep (>5 m) lagoon in the center of the range that can be entered from the east by a large boat but has only a very shallow (0.5-m) cut facing west. The cut can only be crossed by swimming but allows good water exchange when the tide changes and the wind blows from the east or west. The bottom is composed of a thick layer of burrowed mud and the water is usually turbid. Sponge habitats are restricted to hanging and anchored stilt roots from a red mangrove and peat bank along the western flank of the lagoon, on either side of the shallow westward cut.

At Twin Cays, northwest of Carrie Bow Cay (Rützler and Feller, 1987, 1996; de Weerdt et al., 1991; Hajdu and Rützler, 1998) we sampled three sites. One, Hidden Creek, is a 2-m deep, meandering tidal creek that connects an open bay with a shallow enclosed mangrove lake. During each tidal cycle, the water flowing through is either hot and saline (when low tide occurs during a sunny day) or cold and brackish (when low tide occurs during a rainy cold spell) and is exchanged for more tempered open-lagoon water. Values for temperature, salinity, suspended sediments, water flow, and dissolved organics (tannins) can be extreme. Hidden Creek is lined by red mangrove stilt roots and vertical or undercut peat banks covered by sponges. The second site, Cuda Cut, is a short but wide and relatively deep (4 m) passage between the open lagoon and the main channel that separates the two islands that give Twin Cays their name. Water is cool and relatively clear because it is regularly exchanged by tidal and wind currents, with modest sedimentation despite a heavily burrowed, fine-muddy bottom. There are the usual red-mangrove stilt roots and, on one flank, a deeply undercut peat bank with exposed mangrove roots, all covered by sponges. The third site, Sponge Haven, is a shallow (1-m) bay off the main channel and close to its southern exit. Its conditions are intermediate; it is less exposed to wind and is flushed by fresh seawater less often than Cuda Cut. Furthermore, it is not subject to regular environmental extremes, as Hidden Creek is. There are ample mangrove roots and a low-relief peat bank and sponges are plentiful, as the name implies.

Sponge Richness and Abundance

Table 1 provides a preliminary list of the taxa collected and now under study. The list and distributional data are the result of our group survey in August 1997 and are supplemented by a few records obtained during earlier visits (by K. Rützler in 1994, and M. C. Diaz and K. P. Smith in 1996, both unpublished). At this stage, we count 182 species and forms for all seven surveyed localities combined, although only 100 (55%) are readily identifiable. The remaining 45% of the sponges are either new species or morphological variants caused by adaptations to the unusual physical and chemical environment in mangrove ponds or tidal canals. Our sampling locations are comparable in size (each can be surveyed by snorkeling in about two hours) and they appear similar in the biomass of sponges growing on mangrove roots and peat banks. However, they clearly differ in species composition and richness. The Pelican Cays have the highest number of species combined (147 species) as well as per island and pond studied; Manatee Cay has the highest number (95); Cat and Fisherman's cays are second (90) and third (77). Blue Ground Range is next in the hierarchy (54), being richer than each of the Twin Cays sites but not richer than all combined (57). Among the Twin Cays locations, Sponge Haven has the most species (42), Cuda Cut is next (29), and Hidden Creek has the fewest (26).

These mangrove islands provide habitats for 30 very common and quantitatively important sponge species, but the distribution of most is not uniform. Only four species are dominant in all three regions (Pelican, Blue Ground, and Twin): *Tedania ignis, Clathria venosa, Scopalina ruetzleri* (Plate 2e), and *Hyrtios proteus.* Shared exclusively by Pelicans and Blue Ground are three abundant species, *Lissodendoryx colombiensis, Artemisina melana,* and *Mycale arenaria.* Common to both Pelican and Twin cays but rare or not recorded at Blue Ground are *Plakortis halichondrioides?, Spirastrella mollis, Tethya actinia, Haliclona curacaoensis,* and *Amphimedon erina.* Abundant in the Pelicans but lacking or very rare elsewhere are 11 species: *Placospongia intermedia, Monanchora arbuscula, Desmapsamma anchorata* (Plate 2c), *Scopalina hispida, Topsentia ophiraphidites, Callyspongia fallax* (Plate 2f), *Xestospongia carbonaria, X. proxima, Aiolochroia crassa, Aplysina fulva,* and *Verongula rigida.* Exclusive to Blue Ground are four common species: *Acarnus* sp., *Eurypon laughlini, Ircinia campana,* and *Dysidea janiae.* And important at Twin Cays but uncommon or missing elsewhere are *Geodia papyracea, Biemna caribea, Mycale* aff. *magniraphidifera,* and *Halichondria magniconulosa.*

We paired the seven sampling localities and three island regions and compared them with each other using Sorensen's similarity coefficient (Pielou, 1992) (Table 2). The three islands of the Pelican group agree well with each other (between 56 and 61%), as do the three locations within Twin Cays (55–56%). Blue Ground Range does not agree well with the other locations but it is closer to Twin Cays (45%) than to the Pelicans (35%). Comparing Blue Ground with individual sites, Manatee among the Pelicans and Sponge Haven of Twin Cays share the most species (46% and 42%, respectively). The Pelican and Twin Cays (all sites combined) share only

Table 2. Similarity matrix (Sorensen's Coefficient) showing agreement of sponge species (%) collected at all seven localities (and three regions) surveyed. Shadings (dark to none) indicate ≤50%, 40–50%, 30–40%, ≥30% (— = Comparison not applicable.)

		Pelican Cays					Twin Cays			
Localities		Cat	Manatee	Fisherman's	Combined	Blueground Range	Hidden Creek	Cuda Cut	Sponge Haven	Combine
Pelican Cays	Cat	—	60.5	56.3	—	36.1	19.0	23.5	30.3	32.7
	Manatee		—	57.0	—	45.6	23.1	25.8	33.6	36.8
	Fisherman's			—	—	40.0	35.0	37.7	38.7	47.8
	Combined	—	—	—	—	34.8	23.1	23.9	27.5	28.4
	Blue Ground Range					—	35.0	31.3	41.7	45.1
Twin Cays	Hidden Creek						—	54.6	55.9	—
	Cuda Cut							—	56.3	—
	Sponge Haven								—	—
	Combined						—	—	—	—

28% of the species. Broken up into individual locations, Fisherman's Cay has the closest ties to Twin Cays (48%); Cat Cay agrees the least (33%).

DISCUSSION

The primary purpose of our present survey was to determine species richness and frequency of occurrence of sponges in the studied locations. According to our estimates, the Pelican Cays harbor the highest concentration of sponge species and biomass per unit area known to us in the entire Caribbean. At this point we can only speculate on the reasons for this phenomenon. One plausible explanation is that the Pelicans are close to well-developed coral reefs, a reservoir of a diverse sponge fauna that is not as readily available at the other sites because sponge larvae are unable to cross long stretches of uninhabitable environment. Indeed, several of the sponges flourishing in the Pelican ponds—such as *Callyspongia vaginalis, Amphimedon compressa,* species of *Ectyoplasia, Topsentia, Monanchora, Myrmekioderma, Niphates, Xestospongia,* and representatives of the Aplysinidae—are typical of those on nearby reefs. However, even if larvae reach a new habitat they will only settle and survive if circumstances are suitable. Our observations and preliminary data from a previous study (Diaz and Smith, unpublished report 1996) help to clarify some essential environmental differences among the surveyed sites. In order to thrive, sponges require solid substrates for settlement and growth, low sediment exposure to avoid clogging of ostia, modest water movement to prevent silting or physical damage and to provide for food and flushing of waste, and little pressure from space competitors and predators.

Primary substrates in these habitats are mangrove roots, mainly *Rhizophora* stilt roots that are either hanging free or anchored in the bottom, and peat banks, a conglomerate of roots, hair rootlets, detritus, sand, and mud exposed through erosion and in places undercut by currents to form cave-like habitats. Stilt roots are particularly suitable substrates for sponges because they allow settlement over a broad area (offering different light intensities) and depth range (from low-tide level to areas near the silty bottom). Some specialized species with a modest tide range (50 cm) are able to pioneer into the intertidal zone in these mangroves and live and reproduce where sponges are rarely found (Rützler, 1995). Counts of roots (Diaz and Smith, unpublished) reaching below the water surface along the mangrove fringe of the ponds average from 2.2 roots per linear meter at Twin Cays (Sponge Haven) to 3.6 roots/m at Blue Ground Range and 4.2 to 6.2 roots/m in the Pelican Cays.

Peat banks too are most common and best developed in the Pelican Cays ponds. These solid substrates combined with low turbidity account in large part for the greater species richness in the Pelican Cays, although Diaz and Smith report that on a species per root basis, the differences are not pronounced: 1.6 to 2.2 species/root at the Pelicans, versus 1.4 species at Blue Ground, and 2.0 species at Twin Cays. Blue Ground Range, although rich in suitable substrate, is adversely affected by high turbidity and abundant fine sediments that are readily resuspended by storms and other disturbances. At the same time, Blue Ground is rich in sponge biomass and harbors an unusual spectrum of species that seem resistant to the effects of sedimentation and capable of growing to considerable size. With less substrate and moderate turbidity, Twin Cays exhibits comparatively low sponge diversity. Even so, the average number of individuals per root is highest at Twin Cays (4.2, versus 1.9 to 3.4 at Pelicans and 1.6 at Blue Ground), perhaps because of high population turnover related to frequent disturbance by boats and dragging of seines in these heavily fished cays. The surprisingly low turbidity in the Pelican Cays (for Belize-lagoon environments) may be due to the bottom topography of deep ponds and steep honeycomb-like coral ridges, which prevent excessive resuspension of fine sediments during storms and other disturbances.

Of the Pelican Group, Fisherman's Cay is closest to Twin Cays in turbidity and species overlap (47.8%), probably because its ponds (E and F) are small and enclosed, less flushed by open-lagoon waters, and more enriched by organic compounds released from the mangroves. Despite the clarity of the water, there is sufficient food to support dense populations of filter feeders (sponges, ascidians, bivalves, in particular), which depend largely on plankton organisms, bacterioplankton, detritus, and possibly dissolved organics. In addition, sponges probably make efficient use of their resources, through their bimodal pattern of particle retention, which enables them to capture bacterioplankton (0.3 to 1.0 μm) with their choanocytes as well as larger particulate organics (up to 50 μm; eukaryotic cells, microscopically unresolvable organic particles) by phagocytosis in the inhalant canals (Reiswig, 1971).

Competition for space appears similar in all study locations and does not explain sponge-faunal differences between sites. Sponges compete quite successfully in this regard, and many species tolerate overgrowth by other sponges (Rützler, 1970) and by other sessile organisms such as algae, hydroids, and ascidians. Despite the space crunch in some locations, a surprising amount of substrate recently formed or exposed remains unoccupied or undiscovered, perhaps because, as Zea (1993) determined for sponges in Colombian rock and reef habitats, larvae are not constantly released, are weak swimmers, and have a short planktonic life. As recently suggested by Maldonado and Uriz (1999), dispersal by means of embryo-carrying fragments is not an effective alternative in these stagnant pond waters, although fragmentation of embryo-rich sponges does occur in a few species (e.g., *Scopalina ruetzleri*, Plate 2e) under adverse environmental conditions such as temperature stress. This poor dispersal and recruitment ability may also account for local per-root, within-pond, or inside-range variation in sponge composition and abundance (Zea, 1996). Algae, a highly diverse group in these islands (Littler et al., this volume), are strong competitors in many of the habitats studied, particularly since they are not as heavily grazed as on reefs, although the low light levels among the roots and under peat banks slow their growth.

Predation pressure, on the other hand, has only recently been recognized as an important determinant of sponge distribution (Wulff, this volume). The variable ecological setting in near-mangrove environments may influence the abundance of sponge predators such as asteroid echinoderms and angel fish and thus help to explain important differences in the sponge fauna of different mangrove cays.

CONCLUSIONS

The numerous mangrove cays and ranges in the Belize shelf lagoon provide important habitats for marine shallow-water communities. Sponges are a significant part of the fauna: they are rich in species and biomass; provide substrate, shelter, and defense for many other organisms; and affect habitat structure and environmental quality through effective space competition and filter-feeding. The Pelican Cays harbor the most diverse sponge fauna of all the mangrove islands previously visited or studied because of their proximity to the cache of species in nearby reefs. Furthermore, their deep mangrove-fringed ponds provide ample solid substrates, low exposure to sedimentation, and high levels of microplankton suitable for filter feeders. The special topography of steep coral ridges and deep mangrove ponds helps to stabilize sediments in these habitats, which are rich in fine detritus and carbonate mud and sand, even during storms. However, protection from frequent and careless activities by boating, fishing, and snorkeling will be important to preserve the diversity, abundance, and health of these ecologically fragile and delicately balanced communities.

ACKNOWLEDGMENTS

We thank Paul and Mary Shave, Ivan Goodbody, and Mike Carpenter for sharing their knowledge of the Pelican Cays ponds and Larry Manes for acting as station manager and boat captain during the period of our survey. Tony Rath and Jimmy Smith provided invaluable aerial photography of the Pelican Cays. We are grateful to Molly Ryan for drawing navigation maps and Figure 1. British Airways and Trans World Airlines made substantial contributions by donating airline tickets for Belinda Alvarez and Rob van Soest, and for Maria Cristina Dias and Larry Manes, respectively. Sven Zea's work is Contribution No. 157 of the Marine Biology Graduate Program of the Universidad Nacional de Colombia, Faculty of Sciences; and No. 626 of the Instituto de Investigaciones Marinas y Costeras "José Benito Vives de Andreis"–INVEMAR.

Contribution No. 586, Caribbean Coral Reef Ecosystems Program, National Museum of Natural History, Smithsonian Institution.

REFERENCES

Hajdu, E., and K. Rützler
1998. Sponges, genus *Mycale* (Poecilosclerida: Demospongiae: Porifera), from a Caribbean mangrove and comments on subgeneric classification. *Proceedings of the Biological Society of Washington* 111:737–773.

Maldonado, M., and M. J. Uriz
1999. Sexual propagation by sponge fragments. *Nature* 398:476.

Pielou, E. C.
1992. *Biogeography.* Malabar, Fla.: Krieger, 351 pp.

Reiswig, H.
1971. Particle retention in natural populations of three marine demosponges. *Biological Bulletin* 141:568–591.

Rützler, K.
1965. Substratstabilität als ökologischer Faktor im marinen Benthos, dargestellt am Beispiel adriatischer Poriferen. *Internationale Revue der gesamten Hydrobiologie* 50:281–292.
1970. Spatial competition among Porifera: Solution by epizoism. *Oecologia* (Berlin) 5:85–95.
1981. An unusual blue-green alga symbiotic with two species of *Ulosa* (Porifera: Hymeniacidonidae) from Carrie Bow Cay, Belize. *Marine Ecology* 2:35–50.
1990. Associations between Caribbean sponges and photosynthetic organisms. In *New Perspectives in Sponge Biology,* edited by K. Rützler, 455–466. Washington, D.C.: Smithsonian Institution Press.
1995. Low-tide exposure of sponges in a Caribbean Mangrove Community. *P.S.Z.N. I: Marine Ecology* 16: 165–179.

Rützler, K., and I. C. Feller
1987. Mangrove swamp communities. *Oceanus* (Wood Hole) 30(4):16–24.
1996. Caribbean mangrove swamps. *Scientific American*, March, 94–99.

Rützler, K., and I. G. Macintyre (eds.)
1982. Habitat distribution and community structure of the barrier reef complex near Carrie Bow Cay. *The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize* 1: *Structure and Communities*, edited by K. Rützler and I. G. Macintyre, 9–43. Smithsonian Contributions to the Marine Sciences, v. 12.

Vicente, V. P.
1990. Overgrowth activity by the encrusting sponge *Chondrilla nucula* on a coral reef in Puerto Rico. In *New Perspectives in Sponge Biology,* edited by K. Rützler, 436–442. Washington, D.C.: Smithsonian Institution Press.

Weerdt, W. de, K. Rützler, and K. P. Smith
1991. The Chalinidae (Porifera) of Twin Cays, Belize, and adjacent waters. *Proceedings of the Biological Society of Washington* 104:189–205.

Wulff, J. L.
1984. Sponge-mediated coral reef growth and rejuvenation. *Coral Reefs* 3:157–163.

Wulff, J. L., and L. W. Buss
1979 Do sponges hold coral reefs together? *Nature* 281:474–475.

Zea, S.
1993. Recruitment of demosponges (Porifera, Demospongiae) in rocky and coral reef habitats of Santa Marta, Colombian Caribbean. *Marine Ecology* 14:1–21.
1996. Random patterns of sponge distribution in remote, oceanic reef complexes of the Southwestern Caribbean. Abstracts, 8th International Coral Reef Symposium, Panamá, June 24–29, 1996, p. 215.